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RESEARCH

Ecosystem shuffle: the `neutRal` R package to simulate species dance moves

Duccio Rocchini[1]

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Abstract
Understanding how biodiversity patterns emerge from simple ecological processes remains a central challenge in community ecology. Neutral theory provides a parsimonious framework in which species are assumed to be ecologically equivalent and community dynamics arise from stochastic processes such as dispersal, immigration, and speciation. Despite its conceptual simplicity, the spatial implementation of neutral models is often computationally non–trivial and difficult to explore interactively. In this paper I present `neutRal`, an R package designed to simulate spatially explicit neutral community dynamics on a two–dimensional lattice. The package implements a small set of transparent stochastic rules governing local dispersal, global dispersal, and speciation, allowing users to generate and visualize emergent spatial patterns and biodiversity gradients. `neutRal` provides a modular workflow consisting of three core functions: simulation of neutral dynamics, visualization of final spatial configurations, and calculation of biodiversity metrics including species richness and Shannon diversity. Through a series of simulation experiments, I illustrate how `neutRal` can be used to check the influence of the key model parameters on the achieved spatial patterns. By combining simplicity, reproducibility, and spatial explicitness, `neutRal` offers an accessible platform for exploratory research, neutral model construction, and teaching in computational ecology.

Keywords Biodiversity · Community simulation · Computational ecology · Neutral theory · Spatial patterns · Theoretical ecology

Introduction

Ecological communities are complex networks of species interacting with each other and their environment (Bazzichetto et al. 2018). These interactions include competition, predation, mutualism, and other processes that collectively determine the structure and dynamics of the community (Brown 1995). The study of community ecology is essential for understanding biodiversity, ecosystem functioning, and the resilience of ecosystems to external pressures such as climate change, habitat destruction, and invasive species (Hooper et al. 2005; Amici et al. 2015).

Ecological modeling has become a fundamental tool for understanding the dynamics of ecological communities (Chiarucci et al. 2009). Models allow researchers to simulate complex ecological processes and test hypotheses that may be difficult or impossible to investigate empirically (Moudrý et al. 2024). One of the most valuable features of ecological modeling is the ability to simulate and explore scenarios in which environmental conditions or species interactions change, allowing for predictions about future community dynamics under various conditions (Grimm et al. 2005).

Among the different modelling frameworks in community ecology, neutral models have gained prominence as a mechanistic framework in which species are assumed to be ecologically equivalent and community dynamics emerge from stochastic demographic processes (Gotelli 2008). In such models, the dynamics of species spread are driven by random processes such as immigration, random birth and death events, and local dispersal (Leibold and McPeek 2006). Neutral models offer a simple yet powerful

✉ Duccio Rocchini
duccio.rocchini@unibo.it

[1] BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum University of Bologna, Bologna, Italy

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framework for exploring patterns of biodiversity without requiring detailed information about the traits and interactions of species. Obviously, neutral models may not capture all aspects of community structure, but they might provide insights into how random processes and the balance between immigration and speciation can influence biodiversity over time (Hubbell 2001). Moreover, they allow explicit control of key parameters, enabling hypothesis-driven tests on community assembly and comparisons with observed communities (Chave 2004; Holyoak and Loreau 2006).

Simulation approaches provide a practical way to explore the consequences of these neutral processes and to investigate how simple stochastic rules can generate complex biodiversity patterns. Running spatially explicit neutral community models under a simulation framework provides ecologists with a deeper understanding of the fundamental processes driving species dynamics, especially in large-scale or long-term studies where direct observation is not feasible. For example, neutral models are particularly effective in exploring patterns of species distribution across vast landscapes, understanding the role of randomness in species persistence, and investigating the long-term effects of immigration and speciation (Rosindell et al. 2012).

Furthermore, spatially explicit formulations of neutral models provide an important extension of classical neutral theory by explicitly representing the spatial arrangement of individuals and dispersal processes across landscapes (Volkov et al. 2003). Such models allow researchers to investigate how local dispersal, stochastic demographic events, and speciation interact to generate spatial patterns of biodiversity, including spatial clustering, species turnover, and dispersal limitation (Durrett and Levin 1994; Chave and Leigh 2002). By explicitly incorporating space, these models make it possible to explore how simple stochastic rules can give rise to complex spatial biodiversity patterns.

Despite the conceptual importance of neutral models, accessible tools for exploring spatially explicit neutral dynamics remain limited. Many existing implementations focus on analytical formulations or require substantial computational expertise. The aim of this paper is to introduce the `neutRal` package, which provides a simple, transparent, and spatially explicit implementation of neutral community dynamics that integrates naturally within the R ecosystem. Because R is widely used in ecological research for data analysis, visualization, and reproducible workflows, the package facilitates the exploration of neutral models within familiar analytical pipelines.

The specific aims of the `neutRal` package are: (i) to provide a simple framework for simulating neutral species and community dynamics driven by immigration, speciation, and local dispersal; (ii) to allow the exploration of spatial patterns of species distributions under neutral assumptions; (iii) to support the calculation and visualization of biodiversity metrics, such as species richness and Shannon diversity, derived from simulated communities; and, (iv) to offer an accessible tool for educators and researchers interested in neutral theory, spatial ecology, and computational approaches to community dynamics.

The package currently includes three primary functions designed to simulate spatially explicit neutral dynamics and to summarize and visualize resulting biodiversity patterns. These functions allow users to model community dynamics on a grid-based landscape and to explore how stochastic demographic processes influence species distributions over space and time. In addition to the description of the theory and the algorithms of the package, this paper presents example simulations demonstrating how `neutRal` can be used to investigate species distributions and emergent biodiversity patterns under neutral assumptions.

Methods

The `neutRal` package provides a concise framework for simulating and analysing spatially explicit neutral community dynamics. The package is designed to be simple and accessible for both researchers and educators in computational ecology, allowing users to explore the emergence of biodiversity patterns under neutral assumptions.

As previously stated, the package is composed of three core functions:

- `simulate_neutral_grid()` – Simulates the dynamics of a spatially explicit neutral community on a two-dimensional lattice, generating a grid of species identities after a specified number of simulation steps.
- `plot_neutral_grid()` – Based on the `ggplot2` package, it visualizes the final spatial configuration of the neutral community by mapping species identities across the lattice.

- `calculate_diversity()` – Computes biodiversity metrics, including species richness, total number of individuals, and Shannon diversity, from the simulated grid.

Installation

To get the `neutRal` package, one can use the `devtools` package to install it directly from GitHub, as:
`devtools::install_github("ducciorocchini/neutRal")`

Functions

Spatially explicit neutral community simulation by the `simulate_neutral_grid()` function

The `simulate_neutral_grid()` function simulates spatially explicit neutral community dynamics on an $n \times n$ grid over a specified number of time steps. A time step in the function corresponds to a single stochastic update event (i.e., a death–replacement event) affecting one randomly selected cell, and does not represent a fixed ecological time unit such as a year or generation.

The grid is initialized with unique species identities in each cell (maximal diversity), and community composition changes through stochastic replacement events. At each time step, a randomly selected cell is updated either through local dispersal, by copying the species identity of a randomly chosen von Neumann neighbor (von Neumann 1951), or through an immigration event. A von Neumann neighborhood is defined as the set of four orthogonally adjacent cells (up, down, left, and right) surrounding a focal cell on the lattice. During immigration events, a new species can be introduced with probability ν, representing speciation. Optionally, the function allows storing snapshots of the grid at user-defined time intervals.

Because the grid is initialized with arbitrary species identities (maximal initial diversity), the early phase of the simulation may reflect transient dynamics that depend on the initial configuration. Over time, the community approaches a stochastic dynamical equilibrium that is independent of these initial conditions. In practice, it is good practice to allow a burn-in phase before analysing the simulated community. Convergence toward equilibrium can be assessed by monitoring summary statistics such as species richness and Shannon diversity, which are implemented in the `calculate_diversity()` function.

Each update event represents a death-replacement process in which the individual occupying the focal cell dies and is immediately replaced either by local dispersal from a neighbouring cell, by immigration, or by speciation. This update rule corresponds to a spatially explicit implementation of a Moran-type stochastic process, a standard formulation used in neutral community models (Moran 1958). The model follows a zero-sum assumption, where the total number of individuals in the community remains constant (Etienne 2007; Haegeman and Etienne 2008).

The key features of the simulation are: (i) immigration events, which occur with probability m and replace the species identity at a randomly chosen cell by drawing an identity from the current grid (global sampling) - in the current implementation, immigration events correspond to global sampling from the existing community, representing long-distance dispersal within the landscape rather than colonization from an external metacommunity; (ii) speciation, which occurs during immigration events with probability ν and introduces a novel species identity; and (iii) local dispersal, which occurs otherwise and updates the focal cell by copying the species identity of a randomly chosen von Neumann neighbor (up, down, left, right) with periodic (wrap-around) boundaries. The simulation is carried out over a specified number of time steps, with the grid updated at each step. The output includes the final grid representing the spatial distribution of species (algorithm 1). At each time step, a random number is drawn from a uniform distribution to determine whether a global dispersal event occurs with probability m; otherwise, local dispersal is applied. Conditional on a global dispersal event, a second random draw determines whether speciation occurs with probability ν.

Set the random seed to `seed`.
Initialize an $n \times n$ grid with a unique species identifier in each cell (maximal diversity).
Set `next_species_id` to $n^2 + 1$.
Initialize empty containers: `snapshots` and `snapshot_steps`.
for each time step t from 1 to `steps` **do**
    Randomly select a cell (i, j) on the grid.
    if a global dispersal (immigration) event occurs with probability m **then**
        if a speciation event occurs with probability ν **then**
            Assign species `next_species_id` to cell (i, j).
            Increment `next_species_id` by 1.
        else
            Replace the species in cell (i, j) by sampling a species identity at random from the current grid (immigration from the local pool).
        end if
    else
        Select a random von Neumann neighbor (i', j') of (i, j) using periodic boundary conditions.
        Replace the species in cell (i, j) with the species identity found in the neighboring cell (i', j') (local dispersal).
    end if
    if `snapshot_every` is not `NULL` **and** t is a multiple of `snapshot_every` **then**
        Append the current grid to `snapshots`.
        Append t to `snapshot_steps`.
    end if
end for
Return a list containing: the final grid (`grid`), optional snapshots (`snapshots`), the corresponding time steps (`snapshot_steps`), and the simulation parameters (`params`).

Algorithm 1 Algorithm for `simulate_neutral_grid()`

In practice, the algorithm works as follows:

1. **Initialization**: The random seed is set to ensure reproducibility. The landscape is represented as an $n \times n$ lattice in which each cell initially contains a unique species identifier, corresponding to maximal initial diversity. The variable `next_species_id` is set to $n^2 + 1$ and is used to assign unique identifiers to newly speciated lineages.
2. **Iterative dynamics**: The model is updated for a total of `steps` iterations. At each iteration, a single cell (i, j) is selected uniformly at random and updated according to either an immigration event (with possible speciation) or a local dispersal event.
3. **Immigration and speciation**: With probability m, the selected cell undergoes an immigration event.
    - Conditional on immigration, with probability ν , a speciation event occurs and the selected cell is assigned a new, unique species identifier (`next_species_id`), which is then incremented.
    - Otherwise, the selected cell is assigned a species identity sampled uniformly at random from all cells in the current grid, representing a global draw from the species already present in the simulated landscape.
4. **Local dispersal**: With probability $1 - m$, the selected cell is updated via local dispersal. A von Neumann

neighbor (up, down, left, or right) is chosen at random using periodic boundary conditions (wrap-around at the grid edges), and the species identity of the neighboring cell is copied into the focal cell.

5. **Optional snapshots**: If `snapshot_every` is provided, intermediate community states are recorded by storing a copy of the grid every `snapshot_every` iterations, together with the corresponding iteration index. These snapshots allow reconstruction of temporal trajectories without embedding any visualization routines within the simulation.
6. **Final output**: After all iterations are completed, the function returns a list containing the final grid (representing the spatial configuration of species identities), any recorded snapshots and their associated time steps, and the parameter set used in the simulation.

To illustrate the use of the algorithm in practice, the following code runs a spatially explicit neutral community simulation using the `simulate_neutral_grid()` function:

```
#Run simulation
sim <- simulate_neutral_grid(
   n = 80,
   steps = 200000,
   m = 0.01,
   nu = 0.001,
   seed = 1
)
```

This example generates a neutral community on an 80×80 lattice by iteratively updating the grid for 200,000 steps. At each step, the species identity of a randomly selected cell is replaced according to neutral dynamics.

The parameter `m = 0.01` defines the probability of an immigration event, while `nu = 0.001` specifies the probability of speciation conditional on immigration. The random seed is fixed (`seed = 1`) to ensure that the simulation is fully reproducible.

The resulting object `sim` is a list containing the final spatial configuration of species identities across the `(sim$grid)`, together with the parameter values used in

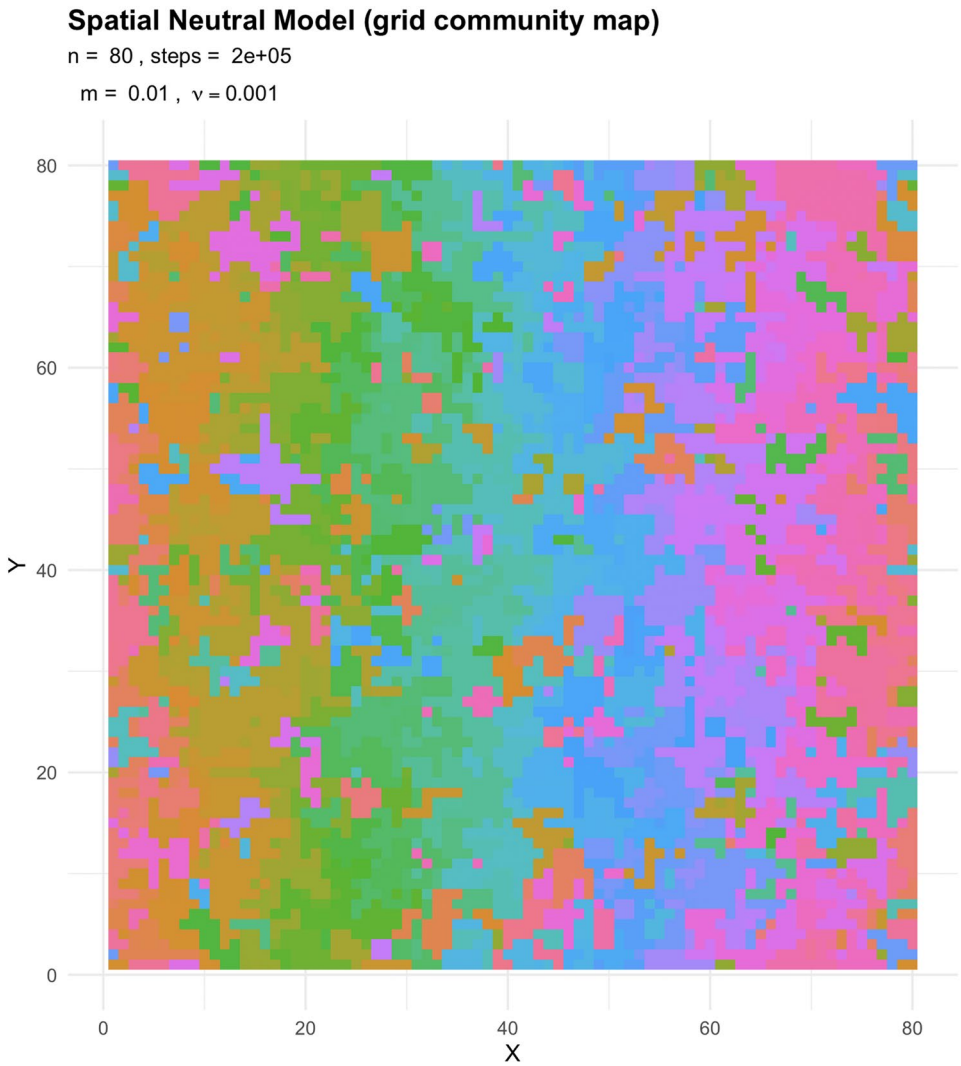

Fig. 1 Species spread on a grid over multiple time steps. Each color represents a different species. A colorblind-friendly version of the figure is available at the `man` page of the `neutRal` package at: https://github.com/ducciorocchini/neutRal/

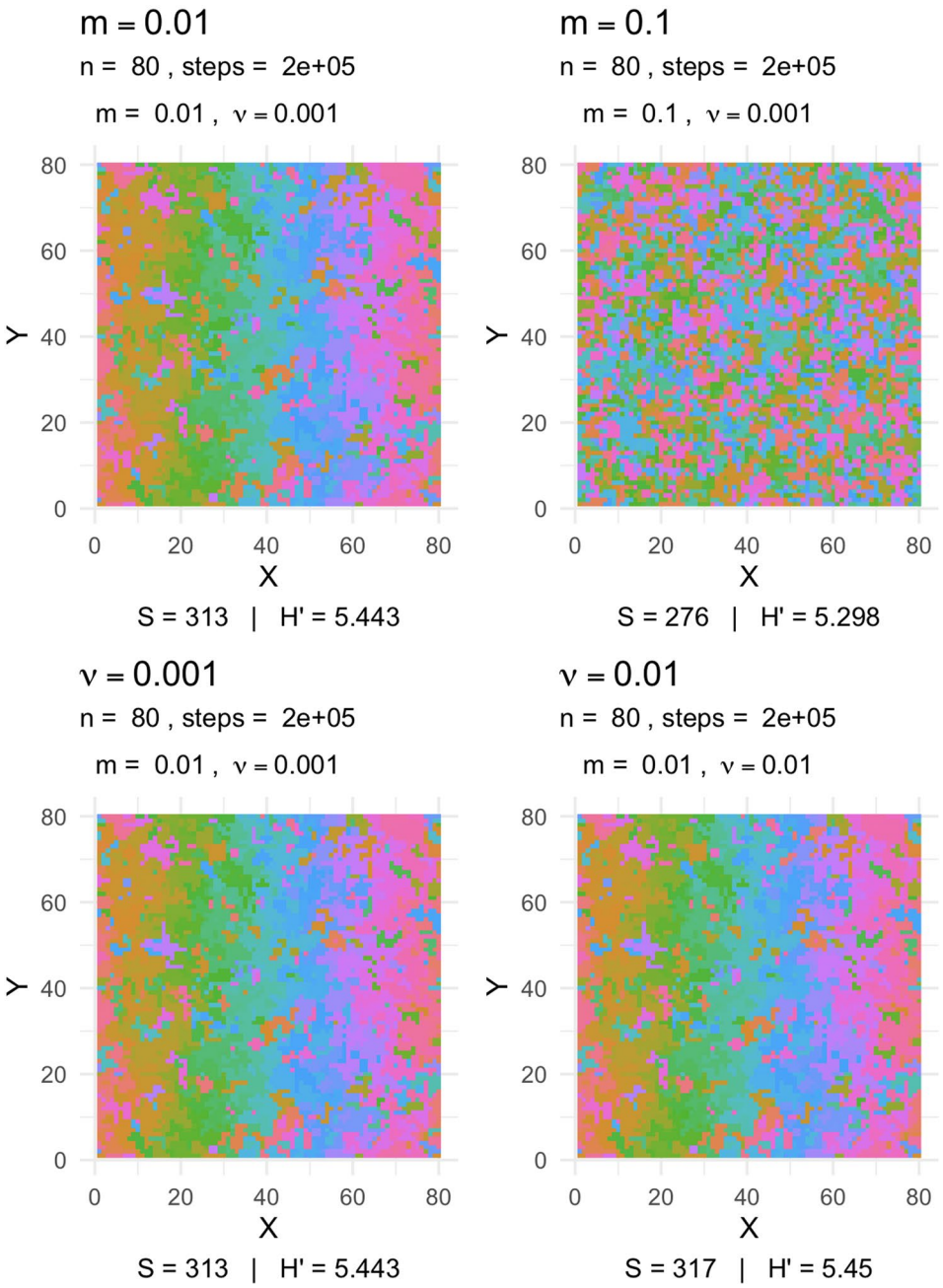

Fig. 2 Final spatial configurations of neutral communities under different values of immigration probability (m) and speciation probability (ν). The top row shows the effect of varying m with ν held constant, whereas the bottom row shows the effect of varying ν with m held constant. For each panel, species richness (S) and Shannon diversity (H') are reported. A colorblind-friendly version of the figure is available at the `man` page of the `neutRal` package at: https://github.com/ducciorocchini/neutRal/

the simulation. This output can subsequently be used for visualization (by the `plot_neutral_grid()` function, subsect, Visualization of simulated neutral communities by the `plot_neutral_grid()` function) and for the calculation of biodiversity metrics (by the `calculate_diversity()` function, subsect, Calculation of biodiversity metrics by the `calculate_diversity()` function).

Visualization of simulated neutral communities by the `plot_neutral_grid()` function

The function `plot_neutral_grid()` provides a graphical representation of the spatial configuration of individuals generated by the neutral model. The community is visualized as a two-dimensional grid in which each cell corresponds to an individual and is coloured according to its species identity.

The input matrix `grid` represents the final state of the simulated community, with integer values identifying species, inherited from the preceding call to the

`simulate_neutral_grid()` function, together with the other parameters: the number of cells n (`params$n`) along each side of the square lattice, the number of steps (`params$steps`), the dispersal probability m (`params$m`) and the speciation rate ν (`params$nu`). The simulation parameters are not required to generate the plot, but are used exclusively to add informative text describing the simulation settings in the final graph. In other words, the simulation parameters in the `plot_neutral_grid()` function serve an annotational purpose rather than a computational one.

Internally, the function converts the simulated grid into a data frame suitable for visualization by expanding the spatial coordinates and associating each cell with its corresponding species identifier. Species identifiers are treated as categorical variables to ensure discrete colour mapping. The spatial layout is rendered using a raster-based approach, preserving the square geometry of the lattice.

The function can be applied directly to the output of `simulate_neutral_grid()`, using the associated simulation parameters to annotate the visualization, as shown below:

```
# Plot final community state
plot_neutral_grid(
   grid = sim$grid,
   n = sim$params$n,
   steps = sim$params$steps,
   m = sim$params$m,
   nu = sim$params$nu
)
```

The resulting plot displays the spatial mosaic of species across the grid (Fig. 1), enabling rapid qualitative assessment of spatial clustering, relative prevalence, and patchiness emerging from neutral dynamics. To emphasize spatial structure rather than individual species identities, the legend is intentionally suppressed.

Calculation of biodiversity metrics by the `calculate_diversity()` function

The `calculate_diversity()` function computes basic biodiversity metrics from the simulated community grid, including species richness (S), the total number of individuals (N), and Shannon diversity `H'`, by:

```
# Calculate biodiversity metrics
calculate_diversity(sim$grid)
```

Using the simulated community generated in the previous example, $S = 313$, $N = 6400$ (namely the squared number of pixels), $H' = 5.443$.

Example simulations using the `neutRal` package

This section provides simple illustrative simulations to demonstrate how the `neutRal` package can be used to explore spatial neutral community dynamics. These examples are intended solely as a practical demonstration of the package functionality rather than as a comprehensive ecological analysis. The link to the complete code is provided in the "Data availability" section below (section 6). As previously stated, in spatially explicit neutral models, community dynamics are typically represented as the outcome of stochastic processes with two key parameters like the immigration probability (m) - influencing the degree of spatial mixing observed in the community - and the speciation probability (ν) - controlling the probability that a speciation event occurs during immigration.

To illustrate how these parameters affect simulated communities, I generated a set of spatial neutral simulations and visualized their final community configurations in Fig. 2, arranged in a 2×2 layout. In the top row, only the immigration probability m is varied while the speciation probability ν is held constant. In the bottom row, only the speciation probability ν is varied while m is held constant. All simulations correspond to the terminal state of an 80×80 lattice after 200,000 update steps.

Importantly, ν does not directly affect dispersal or replacement mechanisms and therefore tends to have a comparatively weaker influence on the resulting spatial configurations (Fig. 2, bottom row).

On the contrary, in these illustrative simulations increasing m (top row) results in greater spatial mixing and reduced persistence of large, contiguous patches formed by local dispersal. As expected, these illustrative simulations suggest that, within the parameter ranges explored here, immigration strongly influences the spatial structure of the simulated community, whereas speciation has a more limited effect on the final spatial configuration.

Discussion

The results presented in this paper demonstrate how a small set of stochastic rules governing dispersal, immigration, and speciation can generate complex spatial patterns, even in the absence of species-specific traits or explicit environmental heterogeneity.

A central result emerging from the simulations concerns the distinct roles of immigration (m) and speciation (ν). Varying m primarily affects the spatial organization of the community, altering the degree of clustering and the persistence of spatial autocorrelation generated by local dispersal.

In contrast, varying ν exerts a comparatively weak effect on large-scale spatial patterns of species distribution (Chave and Leigh 2002; Rosindell and Phillimore 2011). The explicit spatial implementation in `neutRal` makes this theoretical result immediately visible and quantifiable.

From a methodological perspective, `neutRal` occupies a specific niche among ecological modelling tools available in R. Several packages implement neutral or stochastic community models, including `vegan`, `untb`, `EcoSimR`, and `spatstat`. Other spatially explicit community simulation frameworks have also been developed, including the neutral simulator in C++ by (Rosindell et al. 2008), the `MCSim` package (Sokol et al. 2017), the simulation metacommunity framework proposed by Jabot et al. (2020) and its extension to spatial connectivity by Jacquet et al. (2022), the Julia implementation by Suzuki and Economo (2021), or broader spatial ecological modelling frameworks such as the Overview, Design concepts, and Details (ODD) protocol (Grimm et al. 2010), mechanistic simulation models (Cabral et al. 2017), agent-based platforms such as NetLogo (see e.g., Wilensky and Rand (2015); Railsback and Grimm (2019)). Such tools have proven extremely valuable and provide flexible environments for exploring spatial ecological dynamics, offering advanced simulation capabilities. This is particularly useful for exploring neutral theory, neutral model testing, and spatial point pattern analysis. However, such modeling frameworks might require a relatively high level of theoretical or computational expertise.

On the contrary, the primary goal of the `neutRal` package is to provide an easily modifiable spatial neutral model within the R ecosystem, facilitating integration with existing ecological analysis and visualization tools. In practice, `neutRal` emphasizes simplicity, transparency, and pedagogical clarity. The model is fully specified by a small number of intuitive parameters, and the state of the system is explicitly represented as a two-dimensional lattice. This design choice facilitates direct inspection of the simulated community, making it easier to link stochastic rules to emergent patterns. While this simplicity inevitably limits the range of ecological processes that can be represented, it is also one of the main strengths of the package. By lowering the conceptual and technical barrier to entry, `neutRal` makes spatial neutral modelling accessible to a broader audience, including students and researchers new to computational ecology.

Another distinguishing feature of `neutRal` is its explicit separation between simulation, visualization, and analysis. The simulation function returns the full grid state without embedding any plotting or summary statistics. Visualization and diversity calculation are handled by separate functions, which operate directly on the simulation output. This modular structure improves reproducibility and extensibility, allowing users to integrate `neutRal` into larger workflows or to replace individual components with customized alternatives. For example, the output grid can be readily used as input for additional spatial analyses, comparison with empirical data, or coupling with environmental layers.

Although the present paper focuses on neutral dynamics, the framework implemented in `neutRal` also provides a useful baseline for exploring departures from neutrality. Neutral models are often most informative when used as basic expectations against which more complex processes can be evaluated (Chave 2004). In this sense, `neutRal` can serve as a reference model for assessing the added explanatory power of niche differentiation, competitive asymmetries, environmental filtering, or adaptive evolution. By starting from a well-defined neutral baseline, researchers can more clearly identify which patterns require non-neutral explanations (McGill 2003).

The educational value of `neutRal` should also be emphasized. Spatially explicit neutral models are frequently discussed in theoretical ecology, yet their implications are not always intuitive. The ability to interactively modify parameters such as m and ν and immediately visualize their effects can substantially enhance understanding of core ecological concepts, including dispersal limitation, turnover, and the stochastic nature of biodiversity. In teaching contexts, `neutRal` can therefore function as a bridge between abstract theory and tangible spatial outcomes.

Despite its advantages, some limitations of the current implementation should be acknowledged. First, the lattice-based representation assumes homogeneous space and periodic boundary conditions, which may not be appropriate for all ecological systems (Grimm et al. 2005). Second, all individuals are treated as ecologically equivalent, and no explicit environmental gradients or habitat preferences are included (see Bacaro et al. (2015) on the effect of ecological gradients on distributional patterns). These simplifications are inherent to neutral theory (Caswell 1976; Bell 2000, 2001), but they also constrain the range of ecological questions that can be addressed. Users should therefore interpret the results of `neutRal` as exploratory or hypothesis-generating rather than predictive.

Future developments of the package could proceed along several directions. One natural extension would be the inclusion of spatial heterogeneity (sensu (Palmer 2007; Anderle et al. 2023)), for example by allowing dispersal probabilities or immigration rates to vary across the grid (Chase and Leibold 2009). Another promising avenue would be the incorporation of weak niche differences or fitness asymmetries, thereby enabling systematic exploration of the continuum between neutral and niche-based dynamics (Chesson he-2000; Adler et al. 2007; Chase and Myers 2011; Feilhauer et al. 2012). Additionally, tighter integration with spatial

data formats and raster objects would facilitate comparisons between simulated and empirical landscapes.

Another simplification of the current implementation is that the model does not include a distinct regional species pool (metacommunity) from which immigrants originate, as in Hubbell's original neutral theory (Hubbell 2001). Instead, immigration events correspond to global sampling from the existing simulated community. This choice was made to keep the algorithm and its implementation simple and straightforward. However, the absence of an explicit regional pool removes an important feature of classical neutral models, namely the separation of time scales between local and regional dynamics. In models with a metacommunity, species abundance dynamics at the regional scale tend to evolve more slowly than local community dynamics, which can buffer local fluctuations through immigration processes, particularly when community size becomes large. A further step in the development of the package could extend the current framework to include an explicit metacommunity component.

Conclusion

The `neutRal` package provides a compact framework for exploring spatially explicit neutral community dynamics in R. By being released as open-source software, it supports reproducibility, scrutiny, and long-term reuse: users can inspect the underlying assumptions, verify results, and adapt the code to their own systems and teaching needs (Rocchini et al. 2021; von Hardenberg 2025; Uyen et al. 2025). Open development also encourages community contributions, including bug fixes, performance improvements, and extensions to new ecological scenarios, thereby increasing the reliability and longevity of the tool (Rocchini and Neteler 2012). In this sense, `neutRal` is not only a simulator but also a shareable and modifiable reference implementation that lowers barriers to entry for spatial neutral modelling and facilitates comparisons across studies.

At the modelling level, the package relies on a deliberately small set of stochastic rules governing local dispersal, immigration, and speciation. This parsimonious design allows users to investigate how complex spatial patterns and biodiversity gradients can emerge in the absence of species-specific traits or explicit environmental heterogeneity. The results presented in this study confirm that even minimal neutral assumptions are sufficient to generate rich and interpretable ecological outcomes when embedded in a spatial context.

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Author contributions D.R. developed the neutRal R package, designed and performed the simulation experiments, analysed the results, and wrote the manuscript.

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Data availability All data analysed in this study were generated by simulation using the `neutRal` R package. The package is available on GitHub at https://github.com/ducciorocchini/neutRal (development version) and permanently archived on Zenodo with DOI at https://doi.org/10.5281/zenodo.19030070. All simulations and figures presented in this paper are fully reproducible using the example code distributed with the package. The scripts used to reproduce the analyses and visualizations are provided in the package documentation and example files located at https://github.com/ducciorocchini/neutRal/tree/main/man. Colorblind-friendly versions (see Rocchini et al. 2023, Rocchini et al. 2024) of the figures of this paper are available at: https://github.com/ducciorocchini/neutRal/tree/main/man/colorblind_friendly_figures

Declarations

Conflict of interest The authors declare no conflict of interest.

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